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Patterns of Growth and Reproduction in a Natural Population of the Fern *Polystichum acrostichoides*

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ABSTRACT.—Patterns of growth and reproduction were documented in a natural population of *Polystichum acrostichoides* in southeastern Ohio during the 1994 and 1995 growing seasons. The proportion of biomass allocated to fronds increased with plant biomass, indicating fronds are an increasingly dominant component of the body of *P. acrostichoides*. Regression analysis indicated a minimum size threshold exists at which this species first becomes reproductive. Both reproductive status and frequency of reproduction were positively associated with greater plant biomass and above-ground growth rates. A cost of reproduction to growth was apparent; above-ground growth rates increased during non-reproductive years among individuals that reproduced in only 1994. Minor increases in reproductive effort were associated with increasing plant biomass; ranging from approximately 0.01% to 2.11%. Nevertheless, reproductive effort may be plastic in *P. acrostichoides*; the frequency of reproduction correlated negatively with cation concentrations and positively with phosphorous concentrations, and reproductive effort increased with decreasing canopy cover. Together, these observations suggest reproduction in *P. acrostichoides* only occurs when resources are sufficient to offset it's cost to future growth; a life history that may optimize the advantages of early reproduction and life-time fecundity in a species whose colonizing phases (i.e., gametophyte and juvenile sporophyte) have high risks of mortality.

Patterns of vegetative growth and reproduction are major components of plant life history evolution. They are the basis for investigating the relationships between age, size, growth, and reproduction, as well as the roles of genotypic and allometric constraints versus plasticity in allocation patterns (Harper, 1977; Stearns, 1992). According to resource allocation theory, reproduction and growth compete for the same pool of resources and, therefore, occur at the expense of the other (Schaffer and Rosenzweig, 1977; Harper, 1977; Watson, 1984). The size of an individual's resource pool is a function of its capacities for storage and acquisition balanced against its current and past expenditures. Life history theory predicts that, within the boundaries set by genetic and allometric constraints, a species allocation pattern will evolve to maximize it's contribution to the gene pool (Harper, 1977; Stearns, 1992). In populations where juvenile mortality rates are lower than adult mortality rates, selection will favor the demographic advantage conferred by early reproduction. Conversely, in populations where juvenile mortality rates are higher than adult mortality rates, life time fecundity will be favored.

Among angiosperms and gymnosperms, the challenge of studying patterns of resource allocation is compounded by a number of factors, including the existence of structures that serve both reproductive and vegetative functions (e.g., petals, pedicels, bracts, and ovary walls), loss of meristems to reproduc-

tion, production of nectar, and other floral and fruit characters that effect, or are affected by, pollinator visitation and behavior, pollination success, fertilization, and seed set (Harper, 1977; Willson, 1983; Riska, 1986). Because pteridophytes do not produce seeds or flowers, they represent a major group of vascular plants which lack most of the complications listed above. Despite their advantageous simplicity, very little attention has been given to patterns of allocation to growth versus reproduction among pteridophytes, at developmental or ecological levels (but see Raghavan, 1989, and citations therein, regarding development in gametophytes). Moreover, ephemeral, annual, and perennial life histories occur among pteridophytes, permitting study of a variety of life history categories.

This study describes patterns of vegetative and reproductive performance in a natural population of the homosporous fern, *Polystichum acrostichoides* from which hypotheses regarding the life history of this species were developed.

METHODS

Polystichum acrostichoides is an iteroparous perennial that possesses a short-creeping rhizome (i.e., rarely longer than 40 cm) and semi-evergreen fronds that fully senesce as new fronds emerge in the spring. It is a species common to forests of eastern North America and a major component of the understory at the study site, Watterloo Wildlife Research Station (WWRS), Ohio. WWRS is located in Athens County, Southeastern Ohio. The forest at the study site is a mixed hardwood assemblage dominated by species of *Acer, Quercus,* and *Carya.*

To survey the population of *P. acrostichoides* at WWRS, we established two 200 m transects (streambank and upper-slope) in each of three ravines. Upper-slope transects were initiated at points perpendicular in elevation to the beginning of each streambank transect, and were defined as 70% of the elevational distance from streambank to ridgetop. Elevations were determined using a 7.5 minute USGS topographic map (Athens, OH 1985) and an American Paulin Systems model M1-6 altimeter.

An individual plant was identified every 20 m along each transect using the nearest individual method, for a total of 120 plants. To facilitate unobtrusive observation of growth and reproduction during consecutive growing seasons, above-ground morphological measurements (number of fronds, number of fertile fronds, frond area, and fertile area) of each plant were made between mid-June and mid-July, the approximate month of spore release, in 1994 and 1995. Because sporangial maturation is mixed in *P. acrostichoides,* and the inherent difficulty in efficiently collecting spores in the wild, an indirect measure of spore output (i.e., area of the fertile tip of a frond) was used. Fertile pinnae of *P. acrostichoides* occur at frond tips and are densely covered with sori on their lower surface. Separation between fertile and non-fertile pinnae is typically abruptly dimorphic, accompanied by a reduction in size (Fig. 1). Occasionally, the lower-most fertile pinnae are not reduced in size and possess only a few

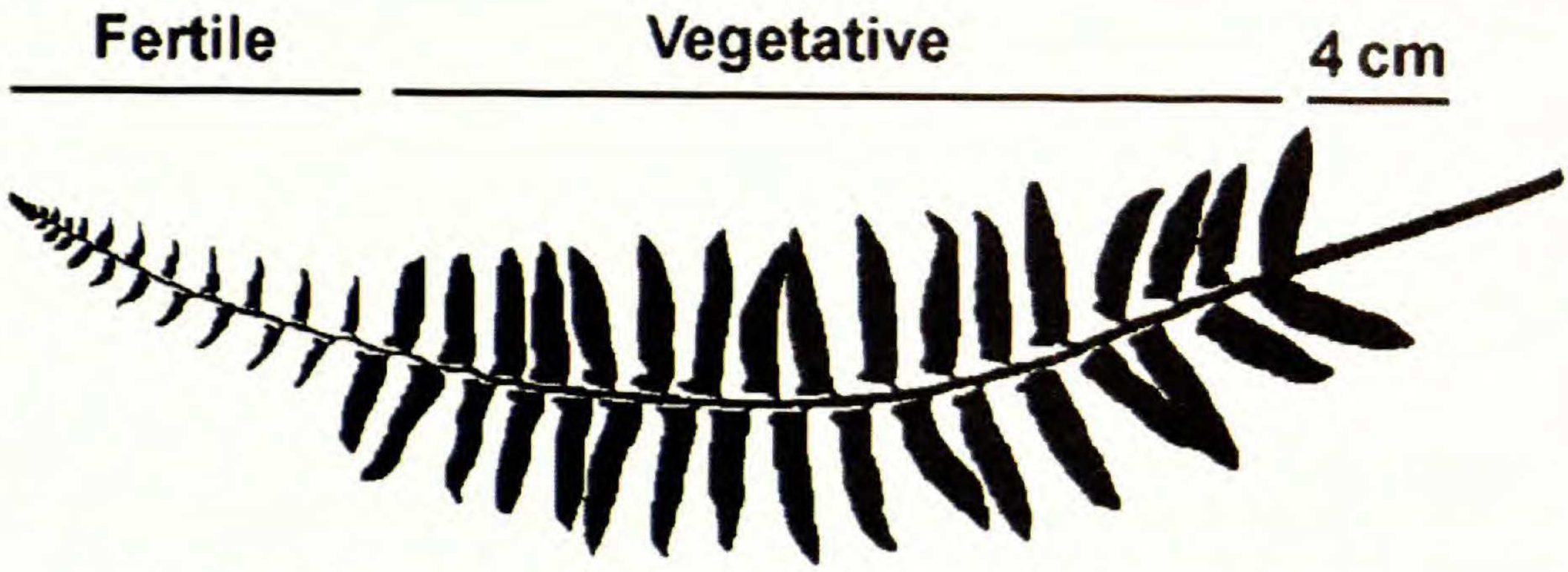

FIG. 1. Silhouette of a fertile frond of *P. acrostichoides* showing the abrupt change in pinnae size between vegetative and fertile pinnae.

scattered sori. To minimize error, these pinnae were not included in the measurement of fertile area. These methods assume the metabolic cost of producing vegetative tissues, sporangia, and spores is relatively constant from year to year (e.g., 1.0 g of spores requires the same absolute metabolic expenditure in 1995 as it did in 1994).

At the end of the 1995 growing season, each plant was collected, stored in a paper bag, dried at 70°C for 72 h, and total frond and rhizome-root mass dry weight determined. Dead rhizomatous tissues and persistent frond bases were removed from the rhizome prior to drying. Eight environmental variables were measured for each plant: canopy cover, moisture status, soil nitrate-nitrogen, phosphorous, pH, and available calcium, magnesium, and potassium. Canopy cover and moisture status for each plant were measured during the summer of 1994. Canopy cover was determined using a Lemmon model-C spherical densiometer. Moisture status was determined using a modified version of the Topographic Moisture Index (Parker, 1982; see Greer et al., 1997 for modification details). Soil was collected in summer 1995 from the rhizome-root mass mantle of each plant, stored in a paper bag, and shipped to the Ohio Agricultural Research Center, Wooster, Ohio, for chemical analysis.

DATA ANALYSES

Spearman's rank (rs) correlations and Mann-Whitney U-tests were used to investigate morphological and environmental differences between non-reproductive and reproductive plants, and between non-sequential and sequential reproducers; i.e., those that reproduced in only 1994 or 1995 versus those that reproduced in both years. Comparisons of plant size and morphology used estimates of 1994 + 1995 plant biomass (total frond + rhizome + root biomass) and mean frond: rhizome-root biomass ratio, respectively, to minimize variance between years. Relative growth rate (reffered to hereon as "growth") was estimated using the equation "(1995 total frond area − 1994 total frond area)/1994 frond area." Environmental variables were represented by loading scores

from Principle Components Analysis (PCA). PCA axes representing more than 10% of total environmental variance, and environmental variables with factor scores greater than 0.50, were interpreted. PCA is sensitive to highly correlated variables within each matrix. Among the environmental variables surveyed, soil pH, available calcium, magnesium, and potassium, were closely correlated, however, removal of all cations except pH did not substantially effect the outcome of the PCA and were therefore retained in both analyses.

Simple linear regressions were used to: 1) explore the relationship between frond and rhizome-root mass biomass throughout development, 2) describe the relationship between plant size and allocation to reproduction versus vegetative growth (i.e., reproductive effort, RE 1), and 3) investigate the cost of reproduction to growth in the following year. RE 1 as well as estimates of above-ground growth, used total fertile area and total frond area to minimize error that would result from conversion to estimates of biomass.

A second measure of reproductive effort (RE 2), based on Willson's (1983) suggestion that a more appropriate measure of reproductive effort for perennials may be yearly allocation to reproductive versus vegetative structures, was used for comparison. RE 2 was estimated for each plant by dividing its 1995 fertile biomass by its change (1995–1994) in plant biomass. Spearman's rank correlations were used to investigate the relationship between reproductive effort and PCA axes representing environmental gradients; mean reproductive effort values were used for each individual (e.g., mean RE 1 = (1994 + 1995 RE 1/ 2)).

The relationship between plant biomass and above-ground growth rate was investigated using linear regression model fitting (SPSS PC+, v. 6.1). Interpretation of regression used to investigate the relationship between reproductive effort and plant size followed Samson and Werk (1986). Their method, which eliminates the autocorrelation that may occur between reproductive biomass and total plant biomass, but also requires untransformed data, permits simple and direct interpretation of the slope and y-intercept. Here, we regressed 1994 + 1995 total fertile biomass against 1994 + 1995 vegetative biomass. To investigate the relationship between plant size and reproductive effort, as defined by Willson (1983) for perennials, we regressed 1995 RE 2 against 1994 plant biomass. Although the potential for autocorrelation exists, total fertile biomass was included within plant biomass for this analysis. Fertile tips typically remain photosynthetic after spore-release (i.e., mid June through early July) and are not reproductive organs. Therefore, deletion of total fertile biomass from estimates of plant biomass would result in under-representation of vegetative biomass.

The D'Agostino-Pearson omnibus test statistic (D'Agostino et al., 1990) was used to determine whether data met requirements of normality. Homoscedascity was tested using the F-max test (Dowdy and Wearden, 1985). All statistics were analyzed using SPSS PC+ v.6.1 (Norusis, 1994). A number of data transformations were used to meet statistical assumptions, including natural log, and power transformations. A critical value of $P = 0.05$ was used in all analyses. All reported r^2 values were adjusted for degrees of freedom.

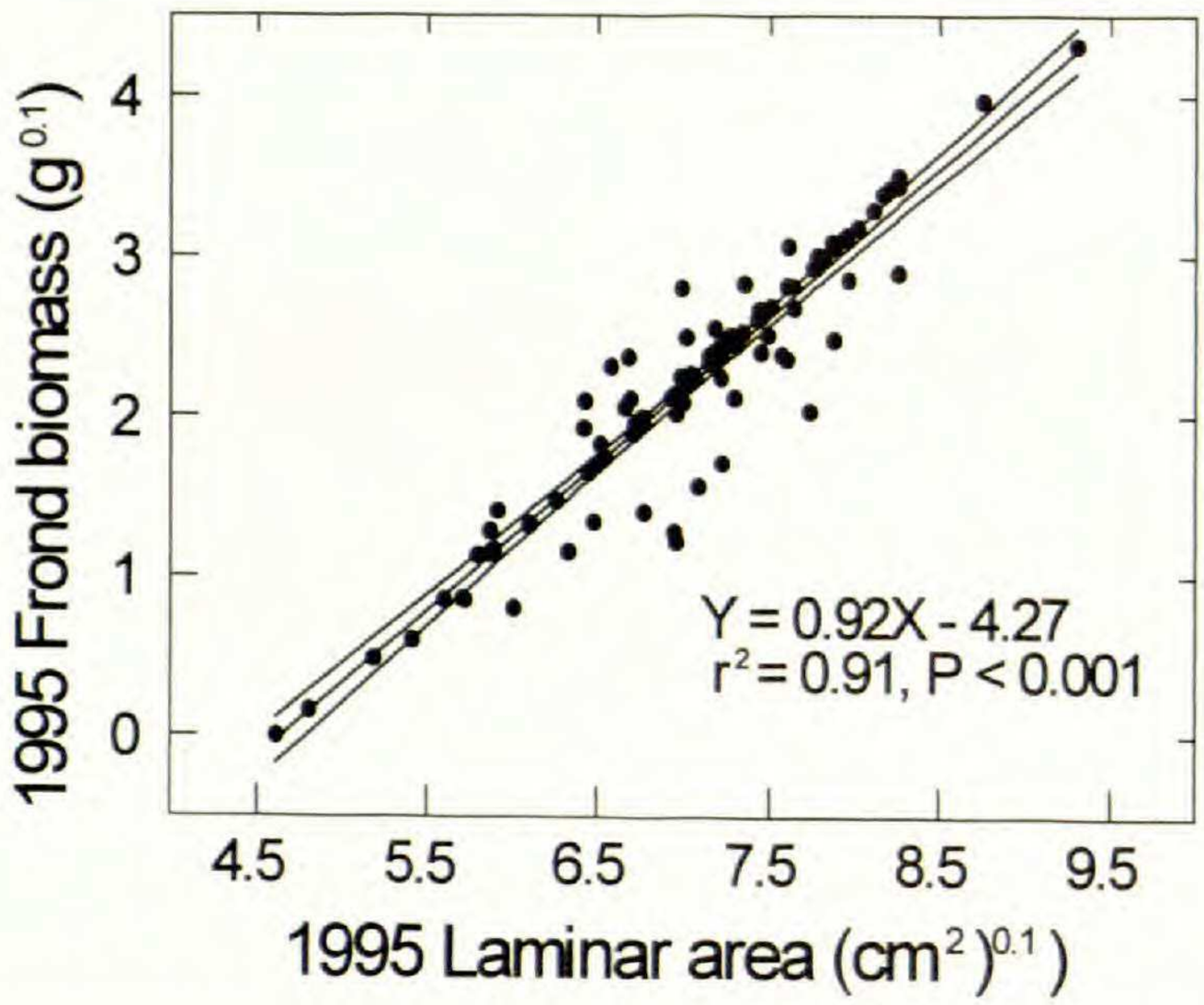

FIG. 2. Regression analysis of 1995 total laminar area (LA) prediction of 1995 total frond biomass (FrB).

RESULTS

Linear regressions indicated frond area and the area of the fertile tip are robust predictors of frond biomass (Fig. 2) and reproductive biomass (Fig. 3), respectively. Consequently, the linear equation "frond biomass = (0.007902 * frond area) − 0.071802" was used to estimate 1994 total frond biomass from 1994 total frond area. Likewise, the linear equation "fertile biomass = 1.85X − 7.66" was used to estimate fertile biomass from fertile area for both 1994 and 1995.

The first four axes from PCA of environmental factors explained 42.2%, 15.3%, 12.7%, and 12.0% of the variance, respectively, for a cumulative 82.2%. The first two PCA axes represented complex environmental gradients; PCA 1 represented calcium, potassium, magnesium, and pH concentrations, whereas, PCA 2 represented moisture and nitrate concentrations (Fig. 4a). PCA 3 and PCA 4 represented canopy cover and phosphorous concentrations, respectively (Fig. 4b).

1994 + 1995 plant biomass correlated negatively with PCA 1 and positively with PCA 4, indicating plant biomass was adversely affected by soil cation concentrations and favorably affected by phosphorous concentrations. Mean frond: rhizome-root biomass ratio did not correlate with any PCA axes (Table 1). Therefore, differences in plant biomass associated with environmental gradients were not associated with differences in biomass allocation to above-ground versus below-ground organs.

Regression modeling indicates growth rate increased with plant biomass and best fit a cubic model (Fig. 5). Gowth rate was associated with changes in frond size as well as frond number. Of 35 individuals that exhibited a decrease in total frond area, 32 (91.4%) exhibited a decrease in frond number. Likewise,

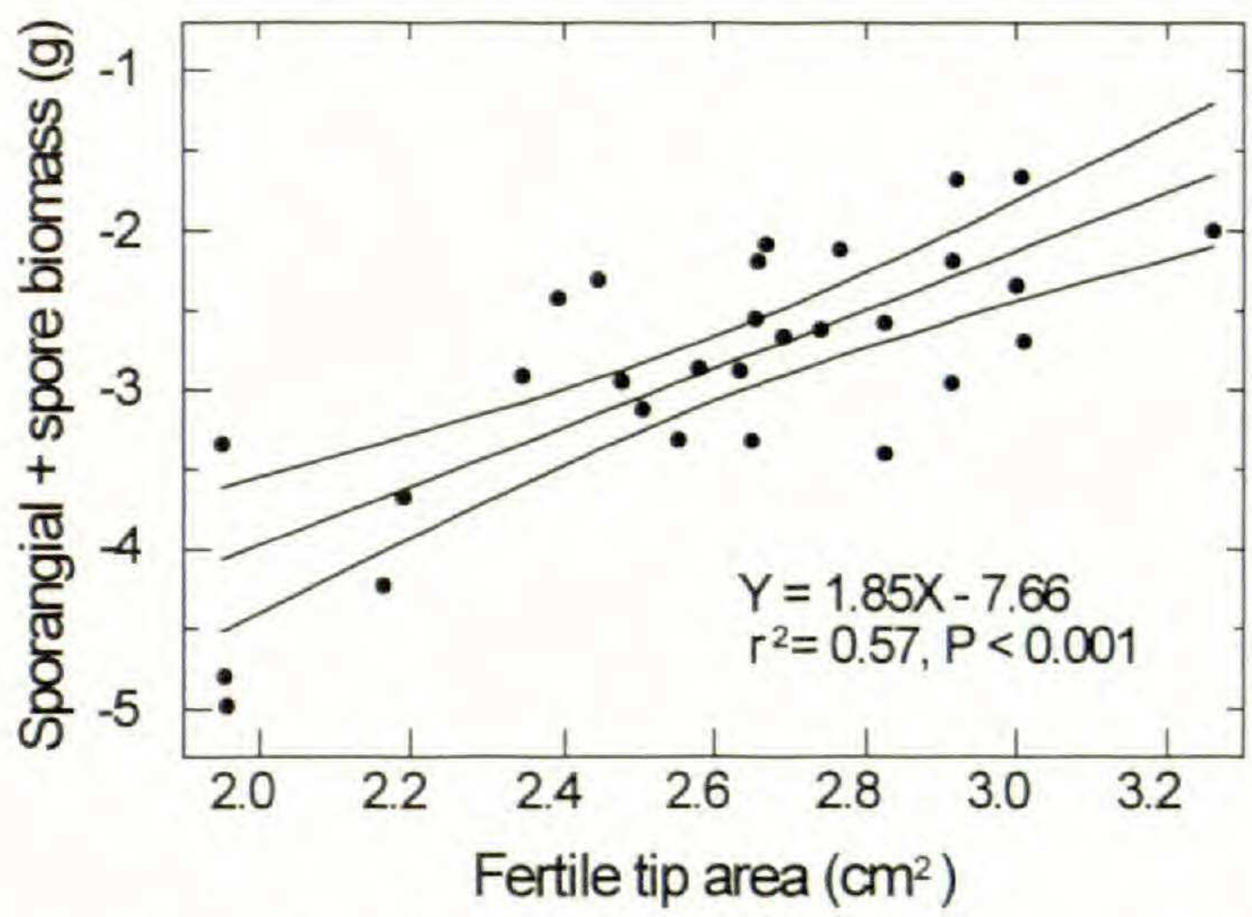

FIG. 3. Regression analysis of total fertile area prediction of sporangial + spore biomass.

54 of 55 individuals (98.2%) exhibited an increase in total frond number. Growth rate correlated significantly and positively with PCA 2 (Table 1), indicating growth increased with moisture and soil nitrate concentrations. However, the low r^2-value indicates considerable variability exists over the range of observations.

The proportion of biomass allocated to fronds increased significantly with plant biomass ($r^2 = 0.31$, $P < 0.001$, $Y = 1.01X - 0.69$). Mean frond: rhizome-root biomass ratio for the entire population was 1.3 ± 1.2, indicating that fronds constituted 56.5% ± 51.7% and rhizome-root mass biomass 43.5% ± 40.2% of plant biomass, respectively. Thus, as plant size increased, allocation shifted from favoring the rhizome-root mass to fronds. As a result, rhizome-root biomass was a poor predictor of frond biomass ($r^2 = 0.19$, $P < 0.001$, $Y = 0.09 + 1.12$).

Of the 120 plants surveyed, 41 (34.2%) were non-reproductive and 79 (65.8%) were reproductive in one or both years. Mann-Whitney U Rank Sum Tests indicate that reproductive individuals were larger (1994 + 1995 plant biomass) and fronds composed a greater proportion of their biomass (mean frond: rhizome-root biomass ratio) than non-reproductives (Table 2). Nevertheless, substantial overlap in plant biomass between reproducers and non-reproducers (Fig. 6) indicates reproduction was not entirely size dependent. Reproducers also exhibited significantly greater growth rates than non-reproducers (Table 2). No significant differences were observed between reproducers and non-reproducers for PCA axes representing environmental gradients (Table 2), indicating their distributions were not influenced by current environmental conditions.

Regression of 1994 + 1995 total fertile biomass versus 1994 + 1995 plant biomass for the entire reproductive population was significant; both slope and y-intercept differed significantly from zero (Fig. 7). The negative y-intercept (−0.29) indicates a minimum size at first reproduction exists in *P. acrostichoides*. Allocation of biomass to reproduction ranged from approximately

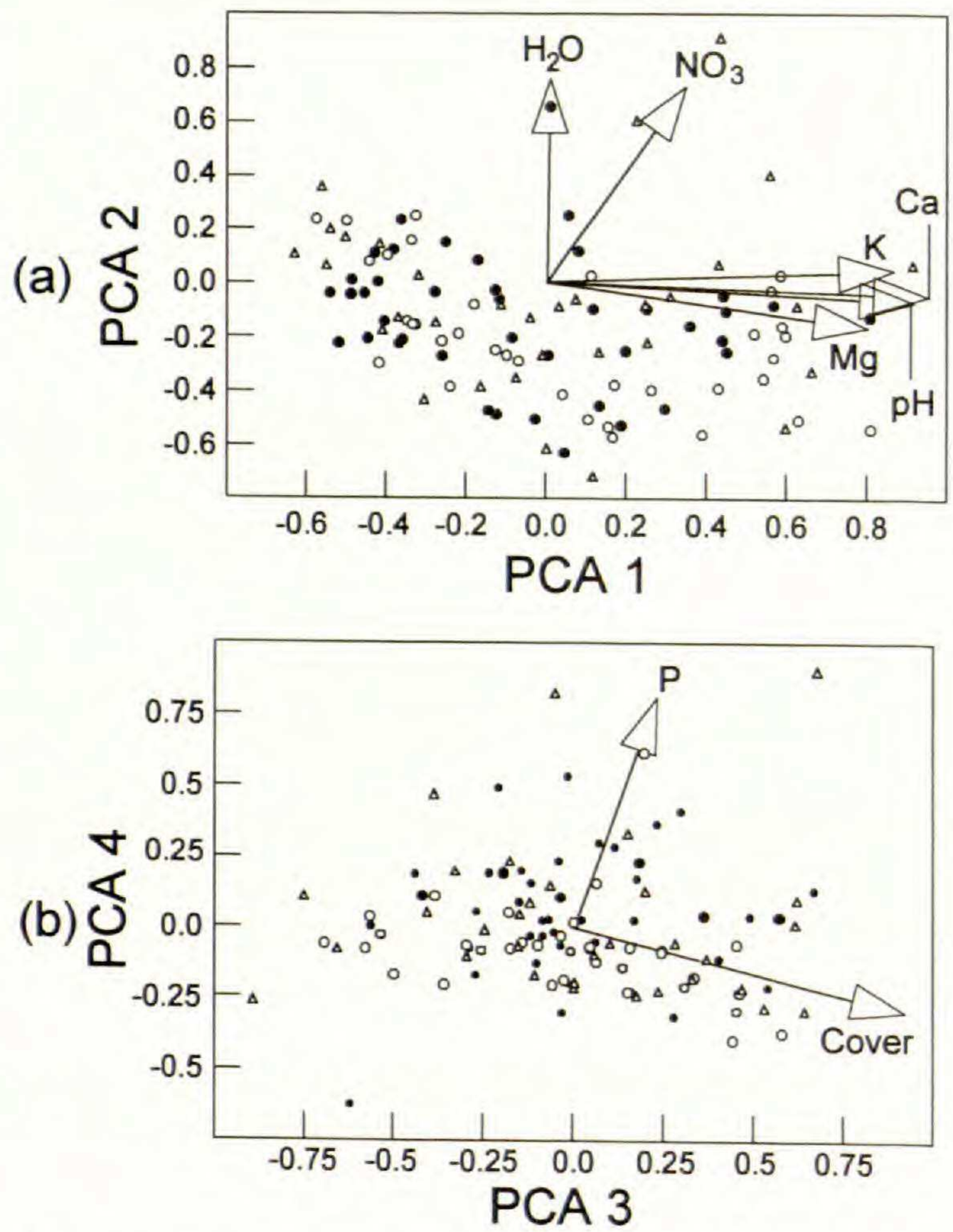

FIG. 4. Ordination from principle components analysis (PCA) of edited data matrix. Arrows indicate strength and direction of environmental gradients based on Spearman's rank correlations between ordination scores and observed environmental values; correlation coefficients can be determined from values on each axis. Symbols represent reproductive status of individual plants as follows: open triangles represent non-reproductives; open circles represent non-sequential reproductives, and closed circles represent sequential reproductives.

0.01% among the smallest individuals to 2.11% among the largest individuals (Fig. 7). The absolute value of the slope was small (0.03) compared to the y-intercept (−0.29), therefore, only a minor increase in the proportion of carbon allocated to reproduction was associated with increasing plant size.

Mean RE 1 and RE 2 correlated negatively with PCA 3 (Table 1). A marginally significant, negative, correlation was also observed between mean RE 1 and PCA 1. These observations suggest allocation to reproduction versus growth decreased with increasing canopy cover, and that soil cation concentrations may have had a small negative effect on reproductive effort.

Of the 79 reproductives, 31 (39.2%) reproduced in only one growing season (i.e., non-sequential reproducers), whereas, 48 (60.8%) reproduced in both growing seasons (i.e., sequential reproducers). Mann-Whitney U Rank Sum Tests indicate sequential reproducers were larger and allocated a greater proportion of their biomass to fronds than non-sequential reproducers; however,

TABLE 1. Spearman's rank correlation coefficients and associated probabilities for morphological traits, measures of above-ground growth, reproductive effort, and PCA axes representing environmental gradients.

TRAIT	PCA 1 (Ca, K, Mg)	PCA 2 (H_2O, NO_3)	PCA 3 (Canopy)	PCA 4 (P)
Plant Biomass (1994 + 1995)	r s^2 = −0.23 P = 0.01	r s^2 = −0.04 P = 0.34	r s^2 = −0.08 P = 0.24	r s^2 = 0.18 P = 0.04
Mean Frond : Rhizome-root Biomass	r s^2 = −0.04 P = 0.36	r s^2 = 0.08 P = 0.22	r s^2 = 0.03 P = 0.39	r s^2 = 0.09 P = 0.21
Growth rate	r s^2 = −0.02 P = 0.49	r s^2 = 0.19 P = 0.04	r s^2 = 0.11 P = 0.16	r s^2 = −0.08 P = 0.23
Reproductive Effort Mean RE 1	r s^2 = −0.17 P = 0.09	r s^2 = 0.16 P = 0.10	r s^2 = −0.28 P = 0.01	r s^2 = 0.09 P = 0.24
1995 RE 2	r s^2 = 0.01 P = 0.46	r s^2s = 0.08 P = 0.29	r s^2 = −0.24 P = 0.04	r s^2 = −0.04 P = 0.39

a substantial overlap in 1994 + 1995 plant biomass indicates that frequency of reproduction was not entirely a function of plant size (Figure 6). Sequential reproducers also grew more rapidly than non-sequential reproducers (Table 3). Moreover, the mean size of sequential reproducers (Figure 6) corresponded with the beginning of an asymptotic increase in growth rate (Figure 5), indicating the ability to reproduce in consecutive years was associated with a high rate of growth.

Sequential reproducers exhibited greater 1994 + 1995 RE 1 and greater RE 2 than non-sequential reproducers (Table 3), indicating, non-sequential reproducers did not compensate for non-reproductive years by increasing allocation to reproduction in reproductive years. Sequential reproducers also exhibited greater growth / 1994 RE 1 than non-sequential reproducers (Table 3), indicating sequential reproducers suffered a smaller cost of reproduction than non-sequential reproducers. Among non-sequential reproducers, individuals that reproduced during only 1994 exhibited greater growth rates than those that reproduced during only 1995 (Table 4). Thus, reproduction was associated with a cost to growth and, subsequently, the probability of reproducing in the following year.

Sequential reproducers possessed lower PCA 1 and greater PCA 4 scores (Table 3) than non-sequential reproducers, indicating environments lower in soil cation concentrations and higher in phosphorus were conducive to reproduction (Figure 4a–b).

DISCUSSION

VEGETATIVE ALLOMETRY.—As sporophytes of *P. acrostichoides* develop beyond an establishment phase, biomass allocation appears to switch from fa-

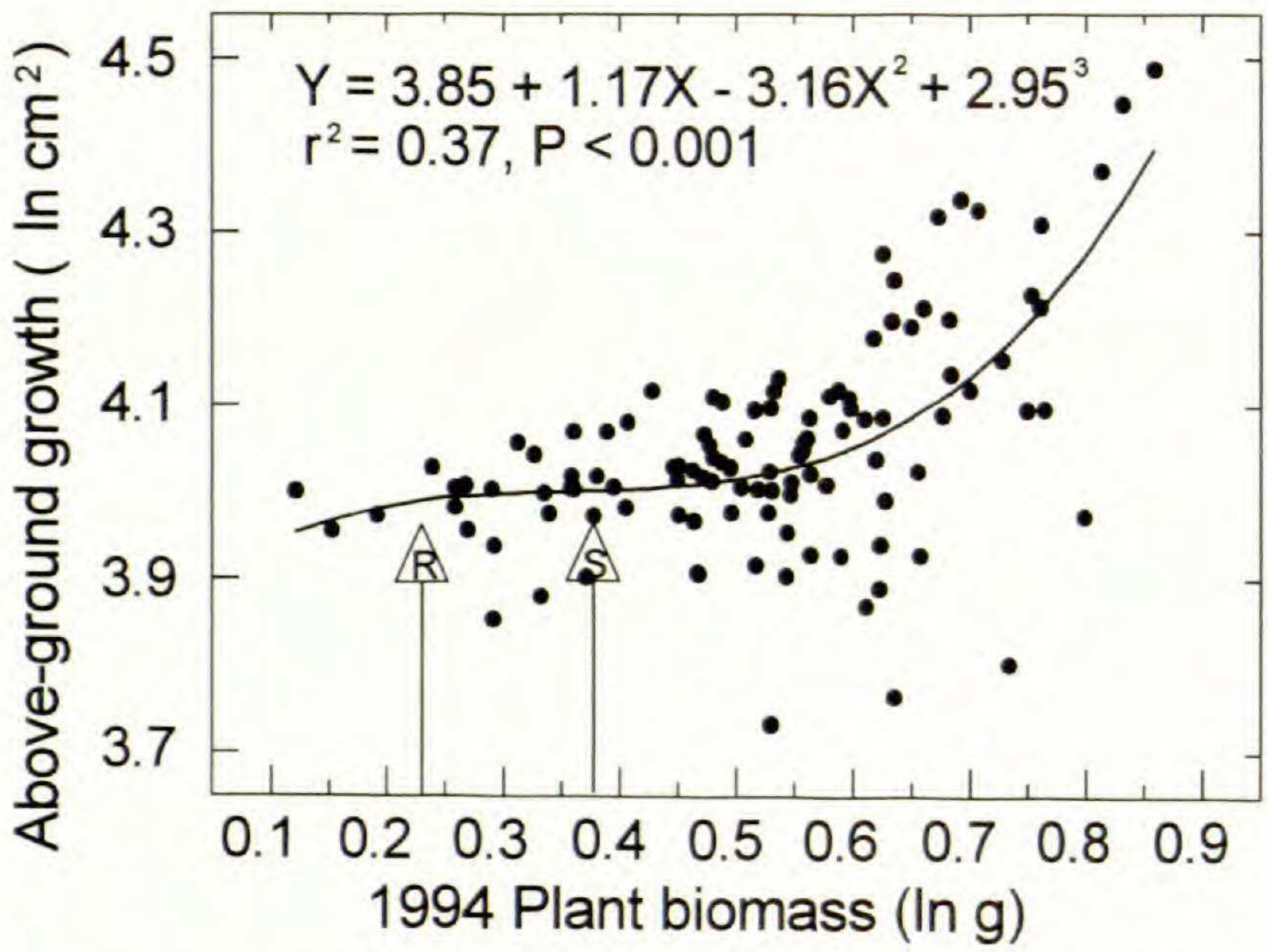

FIG. 5. Cubic model of 1994 plant biomass prediction of above-ground growth rate (i.e., Δ Laminar area). The arrow labeled "R" marks the size at first reproduction determined in Figure 3, whereas the arrow labeled "S" marks the mean size of sequential reproductives (see Figure 6). Growth rates initially increase with plant size during establishment. Reproduction among smaller individuals and/or those in less favorable habitats, may drain resources sufficiently to affect growth, resulting in sporadic (i.e., non-sequential) reproduction and a plateau in growth rates. At some point determined by genotype × environment interactions, resource acquisition and storage may become sufficient to consistently overcome the cost of reproduction to growth.

voring the rhizome-root mass to fronds. The proportion of plant biomass composed of fronds increased with plant biomass; ranging from a 1:4 ratio among the smallest plants to above a 6:1 ratio among the largest plants. The percentage of plant biomass composed of rhizome-root mass reported here (43.5% ± 40.2%) is considerably lower than the 19.0% ± 5.4% root and 60.8% ± 5.8% rhizome reported for this species by Minoletti and Boerner (1993). These differences may have resulted from differences in plant sizes and/or because we removed necrotic tissues from the distal end of the rhizome as well as the relatively large, persistent, frond bases. Early investment to the rhizome-root mass is very likely a trait that has evolved in response to factors that limit survival during establishment. These might include limitation of below-ground resources due to competition, herbivory, environmental composition, fire, and a higher likelihood of above-ground versus below-ground injury.

If biomass also reflects the distribution of most nutrients, then as a *P. acrostichoides* sporophyte develops, the rhizome is superseded by fronds as the primary storage organs. The fronds of *P. acrostichoides* are evergreen, photosynthetically active throughout the year, and a source of metabolites and nutrients throughout the autumn, winter, and spring (Minoletti and Boerner, 1993). Evergreen foliage is important in reducing rates of nutrient loss and in maintaining carbon balance (Aerts, 1995; Jonasson, 1995). The transient nature of fronds, including those that are semi-evergreen, may provide a means for optimizing metabolic expenditures and response(s) to environmental condi-

TABLE 2. Mann-Whitney U rank sum tests of morphological traits and PCA axes representing environmental gradients (see text) between reproductives (R = 79) and non-reproductives (NR = 41). Ranks are ascending.

TRAIT/PCA AXIS	STATUS	MEAN RANK	SUM OF RANKS	U, P-VALUE
Plant Biomass (1994 + 1995)	NR	34.3	1339	U = 559
	R	71.3	5564	P < 0.001
Mean Frond : Rhizome-root Biomass	NR	39.4	1536	U = 756
	R	68.8	5367	P < 0.001
Growth Rate	NR	52.6	2053	U = 1273
	R	62.2	4850	P = 0.08
Reproductive Effort	NR	47.2	1274	U = 832
PCA 1 (Ca, K, Mg)	R	45.5	2912	P = 0.39
PCA 2 (H_2O, NO_3)	NR	51	1377	U = 842
	R	43.9	2809	P = 0.12
PCA 3 (Canopy)	NR	46.8	1264	U = 842
	R	45.6	2922	P = 0.43
PCA 4 (P)	NR	44.0	1189	U = 811
	R	46.8	2997	P = 0.65

tions, and may explain why rhizome-root biomass was a poor predictor of frond biomass. If fronds are the primary storage component in larger plants, then the rhizome may function primarily as a genitor of new fronds and roots. This architectural strategy may be common among fern species with evergreen fronds, particularly those with short-creeping or erect rhizomes.

RELATIONSHIPS BETWEEN PLANT SIZE, GROWTH RATE, AND REPRODUCTION.—Reproduction in *P. acrostichoides* appears to be size dependent. A minimum size at reproduction was apparent; reproducers and sequential reproducers were significantly larger than their respective counterparts, and reproductive effort increased with size. A general relationship between plant size and reproduction has been well established for a variety of species (Sohn, 1977; Pitelka et al., 1980; Young, 1981; Lee and Hamrick, 1983; Willson, 1983; Lacey, 1986; Samson and Werk, 1986; Lotz, 1990; Primack and Hall, 1990; Thompson et al., 1990; Hanzawa and Kalisz, 1993; Linvelle, 1995), and evidence for a minimum size at first reproduction and a relationship between size and frequency of reproduction have been reported for a few iteroparous perennials (Young, 1981; Samson and Werk, 1986; Hanzawa and Kalisz, 1990; Primack and Hall, 1990). Nevertheless, the overlap in plant biomass observed between non-reproducers and reproducers, and between non-sequential and sequential reproducers, indicate reproduction in *P. acrostichoides* is not determined entirely by size.

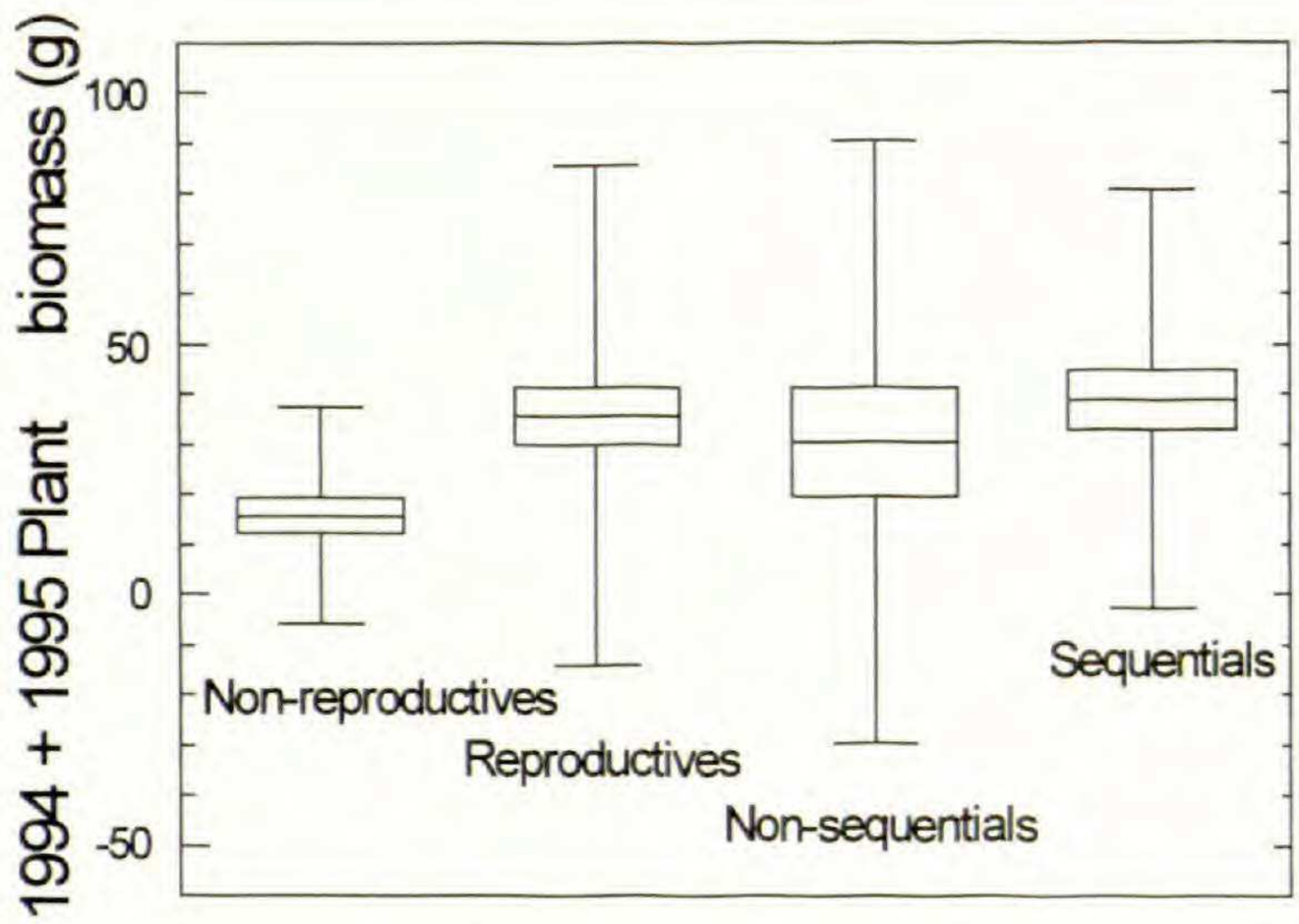

FIG. 6. Box plots of 1994 + 1995 plant biomass (PB) for non-reproductives, reproductives, non-sequential reproductives, and sequential reproductives. Horizontal lines mark the following in increasing order, mean-2*standard deviation, mean-2*standard error, mean, mean+2*standard error, mean+2*standard deviation.

Three observations indicate that reproduction in *P. acrostichoides* occurs only when stored resources exceed that necessary to maintain a threshold rate of growth. First, reproducers possessed higher growth rates than non-reproducers. Second, sequential reproducers possessed higher growth rates and suffered lower costs of reproduction to growth than non-sequential reproducers. Third, a cost of reproduction to growth was evident among non-sequential reproducers; i.e., those that reproduced in 1994 exhibited significantly greater growth rates than those that reproduced in 1995. Similar models of growth-limited reproduction have been suggested for iteroparous perennials by Reekie and Bazzaz (1987c), Saulnier and Reekie (1995), Kozlowski (1992), and Galen and Stanton (1993). According to these models, the curvilinear relationship between growth and plant size may be a function of the threshold of resources necessary for both growth and reproduction.

The value of reproduction is expected to increase with age in iteroparous plants (Kozlowski, 1992; Stearns, 1992). Consequently, iteroparous plants are expected to gradually increase the proportion of resources that are diverted to reproduction with age, or to reach a maximum size, beyond which all resources are diverted to reproduction (Kozlowski and Uchmanski, 1987; Pugilese and Kozlowski, 1990; Kozlowski, 1992; Stearns, 1992; Worley and Harder, 1996). Assuming that size corresponds with age, our observations do not support to these models. We observed no evidence of a maximum size and growth rates increased with size, particularly among the largest individuals. Furthermore, reproduction was sporadic among even the largest individuals, and assuming carbon allocation reflects relative metabolic expenditures (Bazzaz, 1997), only minor increases in reproductive allocation were associated with increases in plant size (i.e., 0.01% to 2.11% of total biomass). Similar patterns of sporadic reproduction and low and/or constant reproductive allocation were reported

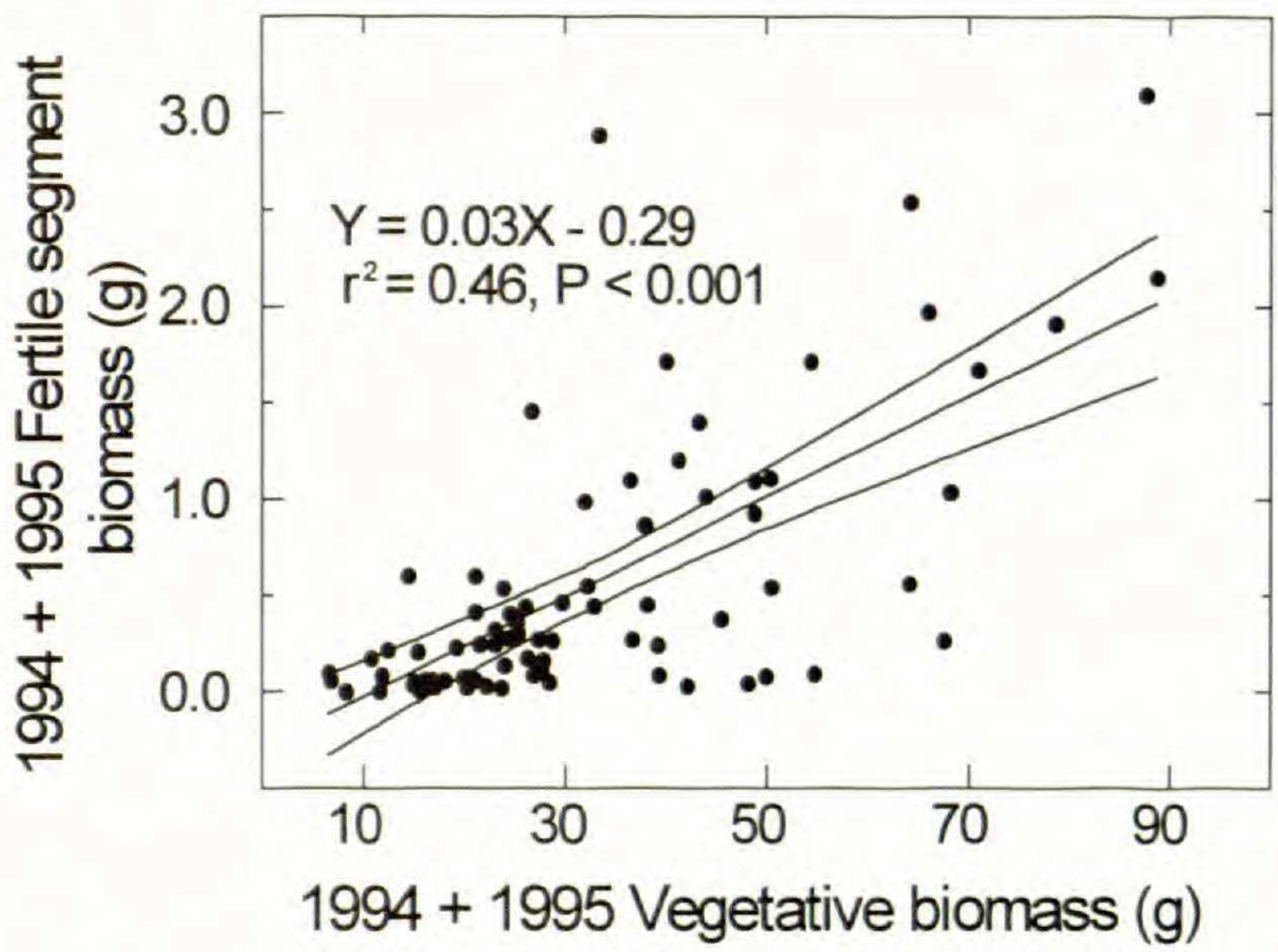

FIG. 7. Regression analysis of 1994 + 1995 vegetative biomass prediction of 1994 + 1995 fertile segment biomass.

for *Chamaenerion angustifolium* (Van Andel and Vera, 1977) and *Cypripedium acaule* (Primack et al., 1994).

Relative construction costs between vegetative and reproductive tissues probably remain constant in most ferns, since they lack the ancillary structures that complicate this relationship (e.g., peduncles, petals, or ovary walls); whether they selectively abort or provision spores is less clear. This is particularly true for species with monomorphic fronds. Nevertheless, life history and demographic traits such as growth, reproduction, and survival, may be more useful measures of the cost of reproduction than limiting metabolic currencies, which are difficult to identify and vary among organs, individuals, populations, and environments (Ricklifs and Miles, 1994; Muir, 1995; Bazzaz, 1997). Assessing the life history and demographic costs of reproduction is also more straightforward for most ferns than seed plants, because, reproduction does not result in the loss of a meristem that could otherwise assist vegetative activity (with the exception of ferns with indeterminate and clone-forming fronds). However, phenological patterns of development may complicate the analysis of resource allocation. Species that reproduce early in the growing season often initiate new vegetative reproductive structures a year or more in advance of emergence (Gerber et al., 1997).

Costs of reproduction were evident among both sequential and non-sequential reproducers as reductions in growth rates and the likelihood of reproducing in the following year. A number of studies have also reported costs of reproduction to survival, growth, the amount of resources allocated to reproduction, and the likelihood of reproducing in the following year (Sohn, 1977; Reekie and Bazzaz, 1987c; Pugilese and Kozlowski, 1990; Fox and Stevens, 1991; Muir, 1995; Worley and Harder, 1996; Gerber et al., 1997). Sporadic

TABLE 3. Mann-Whitney U rank sum tests of morphological traits and PCA axes representing environmental gradients between non-sequential (NS = 31) and sequential (S = 48) reproducers. Ranks are ascending.

TRAIT/PCA AXIS	STATUS	MEAN RANK	SUM OF RANKS	U, P-VALUE
Plant Biomass (1994 + 1995)	NS	30.5	915	U = 450
	S	45.1	2166	P < 0.002
Mean Frond : Rhizome-root Biomass	NS	34.1	1023	U = 558
	S	42.8	2058	P = 0.05
Growth Rate	NS	31.4	942	U = 477
	S	44.6	2139	P = 0.01
Reproductive Effort 1994 + 1995 RE 1	NS	31.9	956	U = 491
	S	44.3	2125	P = 0.01
1995 RE 2	NS	27.4	822	U = 357
	S	36.2	1194	P = 0.03
Cost of Reproduction (Growth rate/RE 1)	NS*	17.5	245	U = 140
	S	35.0	1646	P < 0.001
Environment				
PCA 1	NS	37.2	1005	U = 372
	S	29.1	1075	P = 0.04
PCA 2	NS	30.3	819	U = 441
	S	34.1	1261	P = 0.22
PCA 3	NS	33.0	889	U = 488
	S	32.2	1191	P = 0.44
PCA 4	NS	27.6	746	U = 368
	S	36.1	1334	P = 0.04

* 1994 non-sequentials only; N = 15.

reproduction may be common among plants where reproduction is governed by the maintenance of a threshold rate of growth.

ENVIRONMENTAL EFFECTS ON ALLOCATION PATTERNS.—No patterns in mean frond: rhizome-root biomass ratio were observed relative to environmental gradients. These observations suggest that the developmental relationship between fronds and rhizome-root mass, and therefore investment in to aboveground versus below-ground foraging, may be fairly rigid in *P. acrostichoides*.

In contrast, allocation to reproduction may be plastic in *P. acrostichoides*; reproductive effort correlated negatively with canopy cover, and sequential reproducers were more frequent in habitats low in cations and high in phosphorous. These observations are consistent with the classification of *P. acrostichoides* as a weakly acidophilic understory species (Graves and Monk, 1982;

TABLE 4. Mann-Whitney U rank sum tests of morphological traits between 1994 and 1995 non-sequential reproducers (NS). Ranks are ascending

TRAIT	STATUS	MEAN RANK	SUM OF RANKS	U, P-VALUE
Plant Biomass (1994 + 1995)	1994 NS	15.3	230	U = 110, P = 0.92
	1995 NS	15.7	235	
Mean Frond : Rhizome-root Biomass	1994 NS	16.7	251	U = 94, P = 0.44
	1995 NS	14.3	214	
Growth Rate	1994 NS	19.1	286	U = 59, P = 0.01
	1995 NS	11.9	179	

Greer, et al., 1997) and the hypothesis that reproduction in this species occurs only when a threshold growth rate can be maintained. Given the above, growth rate is predicted to be greatest in habitats characterized by sparse canopy, low cation concentrations, and high phosphorous concentrations. However, no relationship between growth rate and any of these environmental gradients was evident. Increased allocation to reproduction in favorable habitats may have maintained growth rates near a minimum threshold. Plasticity of reproductive effort, resulting in increased sexual and asexual reproduction in favorable habitats, was also reported for *Dennstaedtia punctilobula* (Hammen, 1993).

In contrast to the positive correlation between growth and reprodutive effort among sporophytes, the gametophytes of *P. acrostichoides* increase reproductive effort in habitats that are unfavorable to rapid growth (Greer and McCarthy, 1999). This opposing pattern in plasticity of reproductive effort may be common among species of ferns where the gametophyte is ephemeral and the sporophyte long-lived (Greer and McCarthy, 1999).

A MODEL OF LIFE HISTORY EVOLUTION IN *POLYSTICHUM ACROSTICHOIDES*.—Like many iteroparous plants, the colonizing stages of ferns (i.e., gametophyte and juvenile sporophyte) have much greater risks of mortality than mature sporophytes (Peck et al., 1990). Under these circumstances, fitness is highly correlated with life time fecundity, and the value of reproduction is expected to increase with age (Harper, 1977; Willson, 1983; Stearns, 1992). Nevertheless, rates of reproductive success may be sufficiently low in *P. acrostichoides* and many other pteridophytes, that life time fecundity, and therefore fitness, is maximized through essentially "immortal" life histories that maintain growth across all age classes. Indeed, low reproductive output is favored when environmental heterogeneity affects reproductive success more than adult survival (Murphy, 1968; Pianka, 1972; Schaffer, 1974; Goodman, 1979)—a likely condition among most pteridophytes.

Environmentally induced heterogeneity in recruitment favors plasticity in reproductive allocation (Hirshfield and Tinkle, 1975). Even when conditions that confer a fitness advantage to early or delayed reproduction are infrequent, the onset of reproduction may be optimized through phenotypic plasticity

(Travis, 1994). Thus, plasticity rather than simple allometric relationships may account for much of the variation in age and size at first reproduction (Stearns, 1992), and variation in size at first reproduction may account for much of the subsequent variation in allocation (Samson and Werk, 1986; Herndon, 1987). Physiological and reproductive plasticity that facilitate growth and longevity may explain the wide distribution and abundance of *P. acrostichoides* in Eastern North America.

Although observations from unmanipulated studies of natural populations are ambiguous, this study provides essential baseline data for experimental studies of allometry, resource allocation, and phenotypic plasticity in *P. acrostichoides*.

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